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Title

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<https://escholarship.org/uc/item/6720x050>

Journal

Evolutionary applications, 3(1)

ISSN

1752-4571

Authors

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Publication Date

2010

DOI

10.1111/j.1752-4571.2009.00099.x

Peer reviewed

ORIGINAL ARTICLE

Rapid evolution of morphology and adaptive life history in the invasive California wild radish (*Raphanus sativus*) and the implications for management

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Keywords

aster models, demography, invasive, local adaptation, phenotype, *Raphanus*, reciprocal transplant.

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Received: 7 May 2009

Accepted: 8 August 2009

First published online: 30 September 2009

doi:10.1111/j.1752-4571.2009.00099.x

Abstract

Understanding the evolution and demography of invasive populations may be key for successful management. In this study, we test whether or not populations of the non-native, hybrid-derived California wild radish have regionally adapted to divergent climates over their 150-year history in California and determine if population demographic dynamics might warrant different region-specific strategies for control. Using a reciprocal transplant approach, we found evidence for genetically based differences both between and among northern, coastal and southern, inland populations of wild radish. Individual fitness was analyzed using a relatively new statistical method called ‘aster modeling’ which integrates temporally sequential fitness measurements. In their respective home environments, fitness differences strongly favored southern populations and only slightly favored northern populations. Demographic rates of transition and sensitivities also differed between regions of origin, suggesting that the most effective approach for reducing overall population growth rate would be to target different life-history stages in each region.

Introduction

Invasions often provide examples of rapid evolution, wherein successfully introduced, established and spreading populations become genetically different from populations in a species’ original range (Reznick and Ghalambor 2001; Lee 2002; Bossdorf et al. 2005; Dlugosch and Parker 2008). Genetic drift mediated by stochastic effects in small populations can decrease genetic variation during invasions (Nei et al. 1975), while multiple introductions can enhance it (Lee 2002; Novak and Mack 2005; Sax et al. 2007; Dlugosch and Parker 2008). It is relatively straightforward to demonstrate

rapid evolution resulting from these neutral forces by comparing molecular marker composition in the native and introduced ranges.

Several authors have proposed that rapid *adaptive* evolution in invasive populations is limited or enhanced by the same aforementioned processes. Small-introduced populations lacking additive genetic variation may be unable to respond to natural selection (Lande and Shannon 1996; but see Huey et al. 2005), but multiple introductions (Lee 2002; Novak 2007; Roman and Darling 2007) or interspecific hybridization (Ellstrand and Schierenbeck 2000) may be sufficient to restore adaptive responsiveness to selection (Prentis et al. 2008).

Some evidence suggests that rapid adaptive evolution can enhance invasiveness. Adaptive evolution appears to be associated with range expansion in several species. For instance, the evolution of salinity tolerance and cold tolerance in exotic copepods (*Eurytemora affinis*) in North America and *Rhododendron* in the British Isles, respectively, seems to be related to range expansion (Milne and Abbott 2000; Lee et al. 2003). Latitudinal clines accompany range expansion in St. John's wort (*Hypericum perforatum*), purple loosestrife (*Lythrum salicaria*) and *Drosophila*, all invasive in North America, and in California poppy (*Eschscholzia californica*) in Chile (Huey et al. 2000; Maron et al. 2004; Leger and Rice 2007; Montague et al. 2008). Though rapid adaptive evolution has occurred in each of these systems, whether or not it causes invasiveness *per se* has not been well addressed (but see Lavergne and Molofsky 2007).

The evolution of life-history traits represent several of the best-studied cases of adaptive evolution in invasive populations (Maron et al. 2004; Leger and Rice 2007; Colautti et al. 2009; Monty et al. 2009). These traits, including the timing and duration of reproduction, often show clinal patterns in response to continuously varying conditions like day length and temperature. A detailed study of the rapid evolution of life histories can enhance our mechanistic understanding invasions and also suggest potential management strategies. Often, time and money available for combating invasives are limited, so targeting control of life-history stages that drive population expansion is most efficient (Shea and Kelly 1998; Benton and Grant 1999; Parker 2000). However, if invasive populations have diverged in life-history traits since introduction, the optimal timing of control and stage targeted may very well differ between them (Parker 2000).

Broadly speaking, for rapid local adaptation to occur in any invasive species, several conditions should exist. First, sufficient additive genetic variation for survival and reproduction traits must be present. Second, an invasive must occupy its introduced range long enough to respond to selection. This time-period will vary based on the generation time of the organism and its breeding system (Barrett et al. 2008), among other factors. Third, invasive populations will grow in two or more different habitats in which divergent traits are favored. And fourth, directional selection must be sufficiently strong to outweigh neutral evolutionary forces like genetic drift and gene flow. Recently, Campbell et al. (2009) demonstrated that early generation *Raphanus* hybrids quickly respond to ecologically relevant artificial selection, in some cases, even faster than pure parental lineages. In our system, California wild radish (*Raphanus sativus*), genetic diversity, time since introduction, and selection are all likely sufficient for adaptive response, but the relative strength

of various evolutionary forces is not known. Thus, we have an appropriate and interesting context in which to ask questions about the rapid local adaptation of an invasive species.

Raphanus has an over 100-year history in California. Two species within the genus were introduced to the San Francisco Bay area in the mid-1800's (Robbins 1940; Panetsos and Baker 1967). Based on morphological and genetic evidence, the progenitor parents *R. sativus* (cultivated radish) and the related weed *R. raphanistrum* (Panetsos and Baker 1967; Hegde et al. 2006; Ridley et al. 2008) hybridized to create a stable lineage now known as California wild radish. The current range of the hybrid-derived California wild radish on the West Coast of North America spans from the Baja Peninsula to the northern border of California and beyond into Oregon, and it proliferates in many habitats from coastal dunes to dry inland valleys (DiTomaso and Healy 2006; Hegde et al. 2006; Ridley 2008). California wild radish displays high amounts of neutral genetic variation, likely because of both extensive inter-specific hybridization and multiple introductions (Hegde et al. 2006; Ridley et al. 2008).

Is there local adaptation in California wild radish? Observational evidence in the 1960's first suggested that divergent phenotypes of California wild radish occupied coastal and inland habitats and that this pattern was because of natural selection (Panetsos and Baker 1967). Panetsos and Baker proposed that crop-like populations with a higher frequency of crop traits such as purple and white flowers and swollen roots existed closer to the coast because of suitability to moist, mild environments. *Raphanistrum*-like populations with a higher frequency of traits like yellow flowers and tough, penetrating taproots, on the other hand, existed in the inland valleys because they were better adapted to harsher, dry conditions. Recent statewide study indicates that morphological divergence of coastal and inland populations, though still somewhat evident, appears less consistent than previously described (C. Ridley, personal observation). The adaptive argument for phenotypic divergence was never explicitly tested against a null, nonadaptive explanation that could account for the differences between invasive populations. It is possible and even likely that contrasting introduction histories and/or levels of hybridization have caused invasive populations to diverge in ways that are not adaptive.

This study poses several questions. First, have northern coastal and southern inland populations diverged in California since *Raphanus* introduction and hybridization? Second, has selection-created adaptive differences between populations in these two geographically separate and ecologically distinct areas of the California wild radish range? And finally, can we make management suggestions for

California wild radish based on the presence or absence of local adaptation and information about population life-history and demographic traits?

Materials and methods

Plant material

In fall 2005 and summer 2006, we collected seeds from large (1000+ individuals) California wild radish populations: three in northern, coastal California and three in southern inland California (Table 1). Populations within a region were separated by at least 50 km and no more than 100 km. Regions were separated by over 1000 km. For each population, two nonoverlapping, 25 m transects were laid along which one mature fruit from maternal plants 1 m apart were collected (i.e., 50 fruits were collected per population). Fruits were stored in envelopes in the lab until the time of the experiment.

Description of field sites

The northern, coastal California field site was located at Point Reyes National Seashore (38°02.201'N, 122°57.777'W). This park is unique in that heavy human use, mostly in the form of ranch and dairy operations, has dominated its last 150 years of history. The experiment was set up at an abandoned dairy called 'D Ranch' where non-native species, including ripgut brome (*Bromus diandrus*) and California wild radish are dominant. Generally, wild radish displays a summer annual habitat there; occasionally it appears to survive multiple seasons as a short-lived perennial (J. Digregoria, personal communication). The site's Mediterranean-like climate has cool and rainy winters and warm and dry summers, with wind and fog common year-round. According to the Western Regional Climate Center, the site received over

60 mm of rain during our experiment from April to August 2007.

The southern, inland site was at the University of California Riverside Agricultural Experiment Station in Riverside, CA (33°57.895'N, 117°20.722'W). The experiment station is largely used for research on citrus and other crops. Its disturbed condition with a history of agriculture typifies locations where California wild radish is found in the region. In this site, wild radish is a winter annual. It germinates after late fall or early winter rains and senesces when rainfall ceases and temperatures rise. Total rainfall is low (28 mm during our experiment from February to May 2007) and temperatures extreme, with nearly 100 days per year over 32°C, according to the California Irrigation Management Information System.

Reciprocal transplant design

Riverside, California

On January 3, 2007, we planted and watered in 30 seeds isolated from 30 different maternal fruits per population in flats of sterilized UC Soil Mix III (Matkin and Chandler 1967). Flats were placed in the greenhouses on the UC Riverside campus and watered daily with water containing fertilizer (100 p.p.m. 21-5-20 Peters EXCEL, Grace-Sierra Horticultural Products Company, Milpitas, CA) until seedlings emerged and grew to the two-leaf stage. On January 22, 2007, flats were placed outside overnight to acclimatize seedlings before transplantation the next day. On January 23, we planted five blocks into a disked field at the UC Riverside Agricultural Experiment Station, each block consisting of five replicate plants from the six populations in a complete randomized block design. Only 25 of the original 30 seedlings were used per population. The blocks were five individuals × six

Table 1. Description and location of the six sites from which seeds were collected for the experiment.

Region	Location	Description	GPS coordinates
Northern, coastal California	Sea Ranch Lodge	Unmanaged property between hotel and beach	38°40.805'N 123°25.754'W
	Point Reyes National Seashore (referred to as Study Site)	Abandoned dairy, historically heavy human use	38°02.201'N 122°57.777'W
	Half Moon Bay	Sandy habitat near open beach	37°27.261'N 122°26.409'W
	Johnson Ranch	Former ranch, now undergoing restoration	33°34.132'N 117°04.901'W
Southern, inland California	Hemet	Abandoned field/pasture	33°40.721'N 116°58.720'W
	Riverside	Waste space along railroad tracks	33°58.824'N 117°19.252'W

individuals with 30 cm between plants within a block and 60 cm between blocks. Extra seedlings were planted around the perimeter of the experiment at a distance of 60 cm to reduce edge effects. All seedlings were watered in by hand immediately after transplantation. From January 23 to 26, 30 min of overhead irrigation per day was applied to discourage transplant shock. On February 23, we installed an enclosure around the experiment with $\frac{3}{4}$ " nylon bird netting to protect fruits from predation by house finches. The experiment was periodically weeded by hand.

Point Reyes, California

A similar protocol and identical design were used at the site in Point Reyes National Seashore. Thus, the entire experiment consisted of 300 individuals, 150 at each site. On March 1, 2007, we planted and watered in 30 seeds from the same maternal families used previously in the UC Riverside greenhouses. Seedlings were watered daily with fertilized water until transported to Point Reyes on March 18. On March 19, we mechanically trimmed above-ground biomass in a large area at the field site to remove dense ripgut brome. Most of the shredded plant material was set off to the side. On March 20, we planted blocks and border rows as described above. Seedlings were watered in after transplantation but received no additional irrigation. A 180 cm tall fence was erected around the experiment to protect the plots from trampling by deer and elk. The site was periodically weeded by hand.

Data collection

Data were collected at each site in 1-month intervals until almost all plants senesced. Specifically, we collected data on February 20, March 17, April 18, and May 15 in southern California and April 14, May 13, June 9, July 11, August 9, and September 8 in northern California. On those dates, we recorded life-history stage (rosette, bolting with no flowers, flowering with no fruits, flowers and fruits, only fruits/senesced, or dead), several phenotypic traits including flower color and hypocotyl diameter, and evidence of insect or pathogen attack for each individual. On May 29 and 30, we harvested all above-ground biomass at Riverside and stored the labeled samples in paper bags in a warm, dry facility at the UC Riverside Agricultural Experiment Station. Harvest of individuals at Point Reyes occurred on two occasions to accommodate different rates of plant senescence. On August 8, all senesced plants, approximately half of the 150 individuals, were harvested and transported back to UC Riverside for storage. The remaining plants were harvested on September 8.

After at least 24 h in a 40°C drying oven, samples were processed. Flower number was estimated by counting total number of pedicles. Fruit number was estimated by counting total number of fattened pedicles, which indicates successful pollination and fruit formation. We did not count the actual number of fruits on plants, because the rate of fruit abscission varies dramatically between populations (C. Ridley, personal observation). All fruits (if present) were removed from the dry plant body, and we weighed the remaining material to obtain final dry biomass (g). To estimate seed number, we averaged the number of viable seeds (based on visual inspection) per fruit for 10 fruits per individual and multiplied that number by the total number of fruits as estimated above for that plant. When 10 fruits were not available, we obtained the average number of seeds per fruit using as many fruits as possible.

Data analysis

Phenotypic traits

To compare the ratio of flower color morphs between populations within a region of origin and between regions of origin, we combined data from both field sites and conducted simple chi-square analyses. We statistically compared flowering time using Cox proportional hazards regression implemented in the *R* statistical package (R Core Development Team 2008). This test compares the time to an event (i.e., flowering) between groups and can account for censored data in which an event may occur after the period of observation (Muenchow 1986). We used months to flowering as the dependent variable and region of origin, site, and the interaction between them as the explanatory variables. We compared the diameter of the hypocotyl in the fourth month and final average dry biomass of individuals separately using analysis of variance (ANOVA) in *R* (R Core Development Team 2008). We natural log-transformed both to improve normality of residuals. In each case, we started with a full model, including site, block within site, region of origin, population within region of origin and interaction effects, and used the Akaike information criterion (AIC) to choose the reduced model best fit to the data (Johnson and Omland 2004).

Demography

We constructed a life-cycle graph and corresponding table of transition values for populations with northern versus southern region of origin in each environment based on average monthly, observed transition rates (Fig. 1). We were able to estimate all transitions from the raw data collected, except the transition between seeds and rosettes, which we assume to be 90%. This is a simplifying

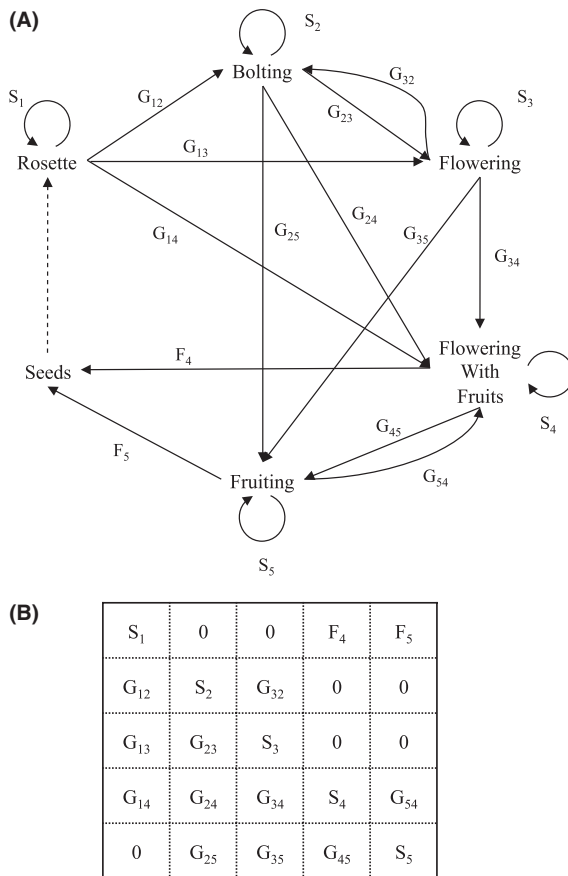


Figure 1 (A) Life-cycle diagram and (B) corresponding table of transition rates estimated from observed data in the experiment. S_i terms are the rates of survival for individual life stages, G_{ij} are the rates of transition from one life stage to another, and F_i are average fecundities for reproductive life stages. Transitions are calculated on a per month basis (see text).

assumption because it does not take into account seed overwintering and subsequent germinability. It is not unreasonable, however, given that we estimated only visually viable seed during our plant processing and that ~90% germination rate has consistently been observed in *Raphanus* under field and greenhouse conditions (Stanton 1984; Mazer 1987; Mazer and Wolfe 1992; Nason and Ellstrand 1995).

We calculated the annual rate of increase (R_0) using the standard equation

$$R_0 = N_{T+1}/N_T$$

where N_T is the size of the population at time T and N_{T+1} is the size of the population 1-year later. We estimated the ratio N_{T+1}/N_T of northern versus southern populations at the Point Reyes and Riverside field sites in

the following manner. We started with an arbitrarily large number of seeds and calculated the number of individuals that would transition to each of the designated life-history stages at the end of month one, given the average transition rates we calculated from the data. With the new distribution of individuals in various life history stages, we calculated the number of individuals in each of the life-history stages at the end of month two, again using the average transition rates. For Point Reyes, we carried out the calculation six times, because the season lasted ~6 months. For Riverside, we carried out the calculation through four cycles, representing a 4-month season. At the end, we multiplied the number of individuals in the fourth stage (flowering + fruiting) and the number of individuals in the fifth stage (fruiting) by the average fecundities for those stages (F_4 and F_5 , respectively) to obtain the number of seeds produced at the end of the season. We multiplied total final seed production by 0.90, to incorporate the assumed 90% germination rate and divided it by the number of seeds we started with to obtain R_0 .

We also devised a sensitivity test to determine which transition rates had the largest effect on the annual rate of increase and whether or not the most sensitive terms differed according to region of origin or environment. For each transition table, we multiplied individual transition rates one at a time by 0.90, effectively reducing the focal transition rate by 10% of the observed value. We then calculated

$$(|(R_{0.90} - R_0)|/R_0) \times 100$$

where $R_{0.90}$ is the annual rate of population increase after reduction in the focal transition rate and R_0 is the original rate of increase, to obtain the percent change in R_0 as a result of alteration of transition terms.

Fitness

To compare the average fitness of individuals from our six populations in each field site, we used a relatively new method called 'aster analysis' (Shaw et al. 2008). This analysis, developed for use in *R*, is a likelihood-based approach with two important features. First, it allows for the joint analysis of fitness variables with inherently different underlying distributions (Geyer et al. 2007; Shaw et al. 2008). Our fitness variables of interest, which served as response variables in the models described below, were survival to flowering, number of flowers, and number of fruits, assigned Bernoulli, zero-truncated Poisson and Poisson distributions in aster, respectively. Adding a fourth fitness variable, number of seeds per plant, to the models caused overspecification (because fruit and seed number were highly correlated), and so we continued the

analysis with only the first three variables noted above. Second, aster analysis accounts for the dependence of one fitness variable on another. In our case, fruit production depends on flower production, which in turn depends on survival to the flowering stage.

We built a series of nested models to test the effects of site, region of origin, population, and population \times site interaction on the response variable most closely associated with evolutionary fitness: fruit number. We also tested the effect of block to examine intra-site environmental heterogeneity. We compared the ability of these models to explain the data using likelihood ratio tests. We were specifically interested in the significance of the interaction between population and site; if an interaction is such that populations produce the most fruits in their home environment, this is evidence for local adaptation. Using the model matrix that best described our data (excluding the 'Block model'), we obtained maximum likelihood estimates and standard errors for fruit number and flower number for each population in Riverside and Point Reyes. Even though the effect of site, region of origin, etc. were not specifically modeled for flower number, their effects on fruit number propagate back to earlier stages and are thus reflected in the estimates (Shaw et al. 2008).

Results

Phenotypic traits

We found significant differences in flower color frequency between northern populations ($N = 106$, $\chi^2 = 63.4$, d.f. = 4, $P < 0.001$), between southern populations ($N = 137$, $\chi^2 = 148.4$, d.f. = 4, $P < 0.001$), and between populations with a northern and southern regions of origin ($N = 243$, $\chi^2 = 29.6$, d.f. = 3, $P < 0.001$). On the regional level, northern California origin tended to have more individuals with purple flowers, while southern

California populations had a rather even distribution of individuals with purple, white, and yellow flowers.

Time to flowering varied significantly with region of origin ($N = 276$, $z = 8.223$, $P < 0.0001$) and with site ($z = -2.841$, $P < 0.01$), but the interaction between them was not significant ($z = 0.571$, $P = 0.57$). Populations with a southern origin consistently flowered earlier than populations with a northern origin at both field sites (Fig. 2). Individuals that did flower, on average, did so later at Point Reyes.

For hypocotyl diameter, we found that the model that best described our data included site, block within site, region, population within region and no interaction effects, with the next best model adding a site \times region interaction (AIC = 381.4 and 382.8, respectively). The average diameter of the hypocotyls in the fourth month varied consistently between northern and southern regions of origin, as well as between populations within a region and between blocks (Table 2). At both field sites, northern populations grew at least 50% larger hypocotyls

Table 2. ANOVA table for best fit model for hypocotyl diameter (mm) and final dry weight (g) as determined by Akaike information criterion analysis (see text).

Factor	d.f.	Ln (hypocotyl diameter)		Ln (final dry weight)	
		MS	F-ratio	MS	F-ratio
Site	1	14.11	4.86	46.61	3.20
Region of origin	1	15.05	9.58***	5.19	0.67
Block within site	8	2.91	13.23**	14.57	9.12**
Population	4	1.57	7.15**	7.79	4.87**
within region					
Site \times region	1	—	—	13.52	8.46*
Error	261, 213	0.22	—	1.60	—
respectively					

** $P < 0.001$, * $P < 0.01$, *** $P < 0.05$.

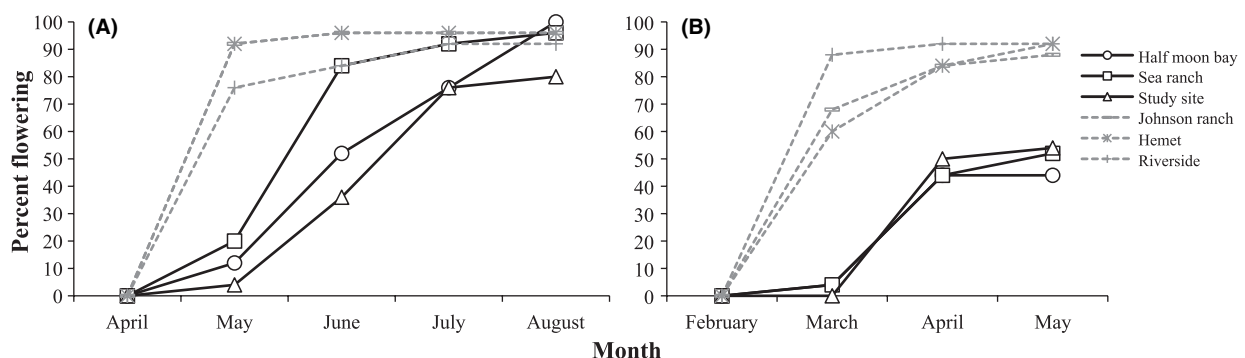


Figure 2 Cumulative percentage of individuals reaching the flowering stage at monthly intervals at (A) Point Reyes National Seashore and (B) Riverside, CA. Solid lines represent populations with a northern origin and dashed lines represent populations with a southern origin.

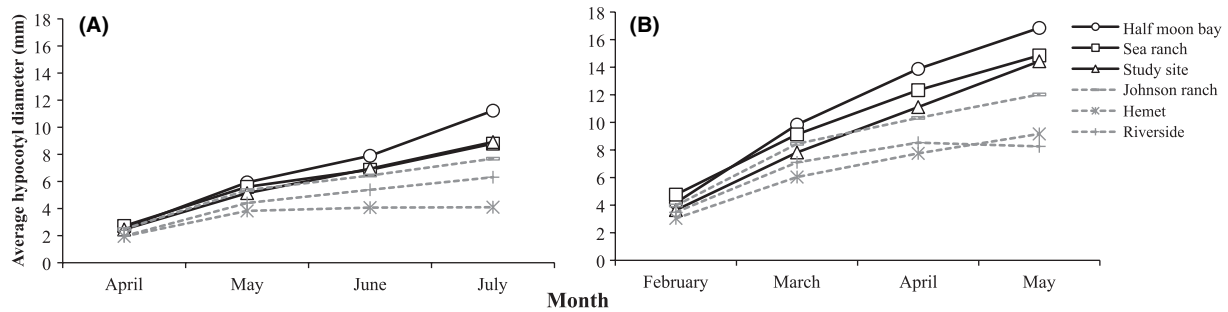


Figure 3 Average diameter of hypocotyls measured at monthly intervals at (A) Point Reyes National Seashore and (B) Riverside, CA. Solid lines represent populations with a northern origin and dashed lines represent populations with a southern origin.

than southern populations (Fig. 3). For final dry weight (biomass), the best model included site, block within site, region, population within region, and a site \times region interaction, and the next best model lacked the interaction effect (AIC = 774.7 and 781.6, respectively). Biomass varied significantly with population and block but not with site or region of origin (Table 2). Plants were on average more than twice as large at Riverside than at Point Reyes by the end of the experiment, and within each site, plants from northern California were more than

twice as large as plants from southern California (data not shown), but significant differences between blocks and populations swamped these effects.

Demography

Estimated annual rates of increase were high for populations with northern and southern regions or origin and across sites. At Point Reyes, northern versus southern populations had an R_0 of 31.4 and 20.5, respectively,

Table 3. (A) Demographic transition and (B) sensitivity tables for pooled populations with a northern or southern region of origin at Point Reyes National Seashore and Riverside, CA field sites.

	Field site									
	Point Reyes National Seashore					Riverside				
(A) Demographic transition rates										
Northern populations	0.631	0	0	44.9	193.2	0.709	0	0	437.3	1558.7
	0.202	0.167	0.055	0	0	0.075	0.167	0.059	0	0
	0.148	0.481	0.26	0	0	0.063	0.042	0	0	0
	0.005	0.296	0.466	0.458	0.016	0.063	0.167	0.353	0.161	0
	0	0	0.151	0.422	0.279	0	0.042	0.353	0.516	0
Southern populations	0.405	0	0	1.164	77.6	0.483	0	0	500.6	1095.3
	0.254	0	0	0	0	0.221	0.15	0.059	0	0
	0.317	0.75	0.058	0	0	0.241	0.525	0	0	0
	0.008	0.125	0.71	0.454	0.051	0.034	0.15	0.353	0.185	0.039
	0	0.031	0.217	0.537	0.532	0	0.075	0.353	0.574	0.263
(B) Sensitivities										
Northern populations	13.4	–	–	1.99	8.01	15.2	–	–	2.27	7.73
	6	1.34	0.55	–	–	1.97	0.38	0.11	–	–
	3.9	4.03	2.86	–	–	3.78	0.29	–	–	–
	0.11	2.51	6.02	6.64	0	4.24	1.47	2.18	1.79	–
	–	–	1.37	6.64	3.18	–	0.32	1.78	5.62	–
Southern populations	7.5	–	–	0.05	9.95	7.13	–	–	1.97	8.03
	4.74	–	–	–	–	4.78	0.65	0.18	–	–
	5.15	4.09	0.7	–	–	4.72	3.59	–	–	–
	0.1	0.59	7.94	6.84	0.051	0.5	1.02	5.29	1.4	0
	–	0.07	1.3	8.58	11.1	–	0.35	2.84	4.83	2.49

Transition terms are as in Fig. 1 and represent average values over populations and months of the experiment. Sensitivities represent the absolute change in the annual rate of increase (R_0) if transitions could be reduced by 10% of their observed value. Largest sensitivity values are highlighted in bold.

while at Riverside, the estimated rates of increase were even higher. Southern populations in their home environment will increase at an estimated rate of 284.1 and northern populations at a rate of 96.0. These rates are likely somewhat inflated given our simplifying assumption that 90% of seeds become rosettes in the next generation.

The total survival (S_i) and growth (G_i) probabilities at each life-history stage for pooled northern versus pooled southern populations favored southern individuals in their home environment (Table 3a). For $i = 1-4$, total transition probabilities for southern populations in Riverside were 0.98, 0.90, 0.97, and 0.76 while northern populations at the same site were 0.91, 0.42, 0.77, and 0.68. These numbers emphasize that the largest difference between northern and southern individuals in Riverside is in the bolting phase ($i = 2$); northern individuals have a much reduced ability to transition out of bolting to the flowering stage. Northern populations did not show an advantage in survival and growth probabilities in their home, northern environment.

Our sensitivity analysis revealed that, for northern populations, R_0 is most sensitive to the survival of rosettes from one month to the next. Reducing this transition by 10% reduced R_0 by 13.4% and 15.2% at Point Reyes and Riverside, respectively (Table 3b). R_0 for southern populations was most sensitive to a change in the ability to remain in the fruiting stage at Point Reyes (11.1%) and fecundity of individuals in the fruiting stage (8.03%) in their home, southern Riverside environment (Table 3b).

Fitness

At Point Reyes, survival was high and comparable between regions of origin. Ninety-two percent of both northern and southern radish individuals survived in this environment. At Riverside, only 70% of northern individuals survived to the end of the experiment in contrast to 95% of southern individuals.

We found a significant effect of site and region on fruit number, as shown by the improvement of the fit of the models when those factors were included (Table 4). Reproduction was consistently lower in the northern site compared with the southern site despite a longer growing season (Fig. 4). Flower and fruit production at Point Reyes was 60% of that in Riverside.

When we compared the nested models with region versus population, we found that population described variation in the data above and beyond that accounted for by region alone. We continued to use population to examine the higher order interaction with site, and found that the interaction was also significant (Table 4).

The signature of local adaptation is apparent when populations have higher fitness in their home environment compared with a contrasting, away environment.

Table 4. Model comparisons to test for the effects of region, population, site and block on number of fruits produced per plant.

Model name	Model formula				
Site × population	Response = stage + site × population × fruits				
Site + population	Response = stage + site × fruits + population × fruits				
Population	Response = stage + population × fruits				
Region	Response = stage + region × fruits				
Null	Response = stage				
Site	Response = stage + site × fruits				
Block	Response = stage + block × fruits				
Model name	Model d.f.	Model deviance	Test d.f.	Test deviance	Test P-value
Site × population	14	-116 8443	5	3051	<0.0001
Site + population	9	-116 5392	1	533	<0.0001
Population	8	-116 4860	4	165	<0.0001
Region	4	-116 4694	1	33	<0.0001
Null	3	-116 4661			
Site + population	9	-116 5392	5	352	<0.0001
Site	4	-116 5040			
Block	12	-117 4112	8	9072	<0.0001
Site	4	-116 5040			

Above are model formulae and below are analyses of deviance; test deviance is twice the log likelihood ratio. Statistical comparisons were made sequentially between nested models. A significant analysis of deviance indicates improvement of the model following the addition of a new factor or interaction, taking into account factors already in the model. Stage refers to life stages included in the aster model described in the text. Parameter estimates for the Site × Population model are presented in Fig. 4.

Using unconditional estimates of flower and fruit production from our 'Site × Population Model,' we found that each southern population produced significantly more flowers and fruits in Riverside than it did in Point Reyes, and that southern populations consistently out reproduced northern populations in their home environment (Fig. 4). The reverse trend was not present. The northern Sea Ranch population produced more flowers and fruits in Point Reyes than in Riverside, and reproduced better than southern populations in its home environment, as we would expect under adaptation to northern, coastal conditions. But the northern Half Moon Bay and Study Site populations did not show this pattern (Fig. 4).

We also found a significant effect of block, likely because of large differences in fruit number between blocks at the Riverside field site. Within the first two months of the experiment, blocks on the east side of the experimental plot were suffering slow growth and reduced size. We measured percent soil moisture on May 10th (towards the end of the experiment), and found that the

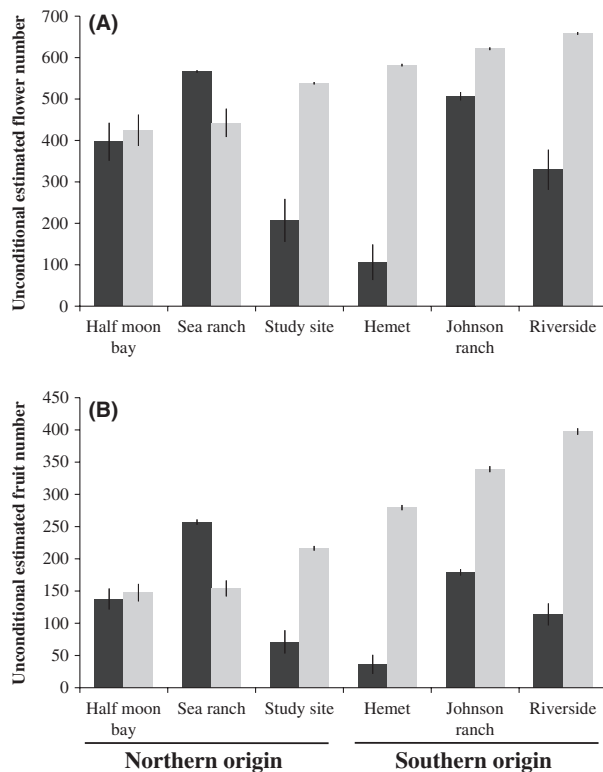


Figure 4 Unconditional maximum likelihood estimates of (A) flower number and (B) fruit number (± 1 SE) for each of the six populations in Point Reyes National Seashore (dark bars) and (B) Riverside, CA (light bars). Values are predicted from the 'Site \times Population' model presented in Table 4.

east side had $\sim 2\%$ soil moisture between 6 and 24 inches below the surface while the west side had $\sim 5\%$ soil moisture at the same depths. Such a small difference in water availability can be important for species composition (Rickard and Murdock 1963) and plant biomass accumulation (Fernandez and Reynolds 2000) in desert-like environments.

Discussion

We found evidence that populations of California wild radish are regionally differentiated in morphological and phenologic traits. Mixed results were obtained for the presence of regionally based local adaptation. A joint analysis of individual fitness traits suggested that southern, inland individuals reproduced better than northern, coastal individuals in their home environment, but that the northern California field site only slightly favored reproduction of northern individuals in their home environment. Estimated population growth rates showed a trend for the annual rate of increase (R_0) to be highest for populations in their home environment, though the

magnitude of the home site advantage was greatest in southern California.

Over 40 years ago, Panetsos and Baker (1967) first described differences between coastal and inland *Raphanus* populations in northern California. Our data reveal that regional differences at a wider, transverse-state scale seem to have developed since then. Hypocotyl diameter, a trait that varies significantly between the progenitors of hybrid-derived California wild radish (Ridley and Ellstrand 2008), also differed consistently between populations of northern versus southern origin. Likewise, flowering time was divergent. Northern populations tended to have delayed onset of reproduction relative to their southern counterparts, reaching $\sim 80\%$ flowering some 4 months into the experiment at Point Reyes, and their reproduction was so delayed in Riverside that about 50% of individuals never flowered. Southern populations, on the other hand, reached high rates of flowering just 2 months after the experiment was planted at both northern and southern field sites.

In addition to regional differences, significant variation also existed between populations within a region with respect to flower color and final biomass. Compared with phenotypic variation described in the 1960's, our populations diverged somewhat less consistently between coastal and inland regions and on a finer scale.

Individual fitness showed significant regional variation, as evidenced by the improvement of fit when region of origin was included in the models describing fitness. Above and beyond the effect of region, population also improved model fit, as did the site \times population term. In Riverside, it was clear that southern populations were better adapted to the short growing season. They produced an estimated 25% more flowers and 50% more fruits per plant than individuals with a northern origin, due in part to their ability to flower and set seed quickly in response to winter rainfall. The evolution of latitudinal differences in flowering time is one of the most often recorded adaptive changes in invasive populations (e.g., Kollmann and Banuelos 2004; Maron et al. 2004; Burger et al. 2007; Leger and Rice 2007). In this study, the effects of latitudinal differences on development time caused by seasonal fluctuations in temperature or light are likely heightened by differences in precipitation between Point Reyes and Riverside. Adaptation of annual species, like California wild radish, to desert and desert-like environments often includes rapid germination and development to reproductive maturity because the availability and seasonal duration of rainfall is limited (Gordon 1989).

At Point Reyes, on average, northern individuals produced more flowers and fruits per plant than southern individuals, but the trend is largely because of one population that was well adapted to its home, northern

environment (Sea Ranch). Interestingly, by September when the last half of the Point Reyes field site was harvested, a number of individuals with a northern origin were still green, demonstrating a previously observed potential capacity to survive to a second season. In fact, the greater investment in plant growth (as revealed by greater final aboveground biomass relative to reproduction and by wider hypocotyls) displayed by northern individuals is consistent with propensity towards perennial habit (Pitelka 1977). In contrast, all individuals with a southern origin senesced by the end of the season. The effect of perenniality on lifetime fitness in this species, therefore, could favor northern individuals in their home environment. Experimentation over several field seasons would be needed to assess this hypothesis.

In sum, we have observed some regional differences between California wild radish populations that are likely adaptive, like flowering time. We also see divergence on a within-region scale, the adaptive nature of which is unknown, but could be tested using reciprocal transplant experiments among population source locations within regions. An additional factor that could also impact variation in traits at the within-region scale is the maternal environment of our field-collected seed. Studies show that seed mass in *Raphanus* can be affected by the environment of the maternal plant (Mazer and Wolfe 1992) and that seed mass can significantly influence seedling size and adult flower production (Stanton 1984). Germination rates were equivalent between all populations of field-collected seed ($N = 410$, $\chi^2 = 10.11$, d.f. = 5, $P = 0.07$), indicating gross differences in seed quality were likely not present, but we cannot rule out the possibility that variation in seeds that germinated could affect the adult phenotype, including fitness, as it does in other systems (e.g., Galloway and Etterson 2007; Donohue 2009). However, at least one recent study indicates that maternal environmental effects are negligible in a rapidly evolving invasive species (Monty et al. 2009).

By what process did California wild radish populations develop divergent, putatively adaptive traits in different regions? Several authors have cautioned the interpretation of evidence seemingly supporting rapid local adaptive evolution in invasive populations (Maron et al. 2004; Dlugosch and Parker 2008; Keller and Taylor 2008). An alternate scenario, namely the introduction of foreign populations into climatically similar or 'matched' environments in the non-native range, can yield a similar pattern of fitness and expected phenotypes without invoking selection (Colautti et al. 2009).

One way to identify the best explanation is to conduct genetic analysis of invasive populations and determine if individuals in contrasting environments within the non-native range are more closely related to each other or to

geographically separated populations in the native range. The geographic genetic structure of invasive population can also give insight into whether or not control of an invasive's spread should be focused on established, spreading and evolving populations or new and potentially ongoing introductions. In case of California wild radish, climate matching of introduced populations to locations similar to those in their native range is unlikely for several reasons. First of all, genetic evidence shows little to no geographic structure of introduced cpDNA haplotypes within California despite such structure in their home range (Ridley et al. 2008), suggesting particular *R. raphanistrum* populations or varieties of cultivated radish have not established under specific preadapted conditions as would be expected under a climate-matching scenario. Genetic markers with greater resolution may better resolve this issue. Second, all populations of California wild radish appear to be hybrid-derived (Hegde et al. 2006; Ridley et al. 2008), possessing reshuffled and unique combinations of alleles not found in either progenitor species. Even if preadapted genotypes of *R. raphanistrum* or cultivated radish had originally established in particular locations within California, extensive sexual reproduction between the two parental species likely would have broken them down. Notably, the high levels of genetic variation and the obligately outcrossing breeding system of *Raphanus* may have facilitated the rapid evolution of local adaptation in California, as they have for other species (Barrett et al. 2008).

Even if our study shows a trend for the presence of local adaptation in an invasive species, we do not necessarily conclude that rapid local adaptation contributes to invasiveness *per se*. Phenotypic plasticity, in which individuals perform generally well in many environments as opposed to especially well in a local environment, has long been hypothesized to confer weediness (Baker 1974) and more recently invasiveness (Daehler 2003). Some evidence supports plasticity as a mechanism for invasion in plants (Daehler 2003; but see Hulme 2008; Keller and Taylor 2008); in fact, individuals from one of our populations, Johnson Ranch, seemed to display plasticity by maintaining relatively high reproductive output across our two field sites.

Clearly, adaptive evolution increases fitness over generations. Increased reproduction can lead to enhanced propagule pressure, which seems to be highly correlated with invasion (Lockwood et al. 2005; Colautti et al. 2006; Hayes and Barry 2008). Future study examining the link between evolution and invasion will undoubtedly involve experimental evolution approaches. It is necessary to compare the invasive qualities of evolutionarily responsive populations to those constrained in their ability to evolve. One such study of weedy annual cocklebur (*Xanthium*

strumarium) mimicked evolutionary changes in phenology and showed that induction of earlier flowering enabled individuals to survive and reproduce outside their current invasive range in North America (Griffith and Watson 2006). Studies of how evolution affects not only individual fitness but also dispersal are sorely needed as well.

Whether or not rapid local adaptation facilitates invasion, its presence does have bearing on how we choose to manage invasive populations. For invasives that are relatively genetically uniform and have little potential to locally adapt, we might find the susceptibilities of common genotypes and exploit them throughout their geographic range (Van Driesche and Bellows 1996; Sakai et al. 2001). Invasive species that have the capacity to evolve rapidly or that are represented by introductions of divergent genotypes to different areas will require different management approaches. Populations that are established as diverse and/or evolving invasive lineages will likely require region-specific strategies, monitoring of control efficacy and adaptive management for long-term successful control.

From the information we included in our demographic analysis, populations of California wild radish should be expanding, almost out of control. Population growth can be represented several ways, and calculating annual population growth rate (r) $\ln(N_{T+1}) - \ln(N_T)$ where N_{T+1} is the number of individuals 1 year in the future and N_T is the number of individuals in the present population, our estimated r values are between 3.12 and 5.75, not wildly higher than we have previously estimated for *Raphanus* hybrids in a Michigan field site (Campbell et al. 2006). Population growth rate was not sustained at this level over time, however, likely a result of density effects. Density can reduce survival and the total seed mass produced by *Raphanus* plants (Mazer and Wolfe 1992) and reduced individual seed mass can in turn lower germination rates (Stanton 1984). In its invasion of California, wild radish may have been able to disperse seeds away from explosively growing populations to limit the effects of density. This scenario is certainly consistent with the spread of an invasive species, although further study would have to be conducted to examine the effect of density on dispersal. We also acknowledge that, in addition to differing density effects from year to year, environmental variation could impact population demography. Our data from a single year could be followed up with similar data in subsequent years to determine consistency of observed transitions and sensitivities over multiple seasons.

Control of *Raphanus*, should it be pursued in California, would be most efficient if pursued in a locally appropriate way. For instance, in both northern and southern populations in their home environment, reducing fecundity (F_5 , specifically) would have a large impact on popu-

lation growth, but because populations in these regions have diverged for life-history characteristics, reducing seedling survival would have an even greater impact on limiting northern population growth. If resources for control are limited, this might mean releasing seed bio-control agents in southern California versus applying herbicides to seedlings early in the season in northern California. The reality for *Raphanus* and other evolving invasive species, however, is that their strategies for management will likely have to adapt as they do.

Acknowledgements

The authors would like to thank the staff of the Agricultural Experiment Station at the University of California Riverside, the National Park Service, and a host of Ellstrand lab members for assistance in the field. C. Geyer, R. Marushia, H. Regan, and R. Shaw provided advice on data analysis. The research described in this paper was performed by C.E.R. in partial completion of her PhD requirements and was funded by the U.S. Environmental Protection Agency (EPA) under a Science to Achieve Results (STAR) Graduate Fellowship. EPA has not officially endorsed this publication, and the views expressed herein may not reflect the views of the EPA.

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